Preliminary cladistic analyses of relationships among loliginid squids (Cephalopoda: Myopsida) based on morphological data

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Abstract: Most species in the cephalopod taxon Loliginidae have a near-shore habitat and are commercially important, yet phylogenetic relationships within the group have not been examined. In this study, relationships among loliginid species are analyzed using cladistic methods. Forty-eight morphological characters for 48 species (40 loliginid species and eight outgroup taxa) were collected through examination of museum specimens and primary literature and coded into a matrix for cladistic analysis. Both unweighted and successive weighting maximum-parsimony analyses were undertaken, and the phylogenetic signal of the data was evaluated. Unweighted analyses support the hypothesis of monophyly for Loliginidae, and suggest some well-supported sister species and crown-clade relationships (such as *Alloteuthis* Wülker and *Sepioteuthis* Blainville), but the positions of these groups relative to one another cannot be resolved due to the large number of most-parsimonious trees. Successive weighting analyses showed support for some additional major clades (*Photololigo* Natsukari and *Nipponololigo* Natsukari), and provided insight into the cladistic information value of the characters in the analysis. Continued collection of morphological and internal anatomical data for these species for all stages of the life cycle, as well as the addition of molecular data to the analysis, could help resolve relationships within the group.

The cephalopod taxon Loliginidae contains over 40 species of neritic squids found on most tropical and temperate continental margins around the world (Roper *et al.*, 1984). In many regions, these squids are found in high abundance near shore, particularly when spawning, and some species form integral links in coastal marine ecosystems (such as *Loligo opalescens* Berry, 1911, in Monterey Bay, California; see Morejohn *et al.*, 1978). Many loliginid species are commercially harvested (Roper *et al.*, 1984). In addition, the giant axons of certain loliginids (such as *L. pealei, L. vulgaris*, and *L. opalescens*) have served as important model systems in neurophysiological research (*e. g.* Young, 1938; Gilbert *et al.*, 1990; Rosenthal and Gilly, 1993).

Despite the ecological, economic, and scientific importance of loliginid squids, their phylogeny remains unresolved, and their taxonomy is confused (Voss, 1977). Numerous recent works (Natsukari, 1983, 1984; Brakoniecki, 1986; Alexeyev, 1992; Vecchione *et al.*, in press) have sought to clarify loliginid taxonomy using key morphological characters. Brakoniecki (1986), who examined loliginid hectocotylus morphology, grouped the species he studied into six hectocotylus types. He based a new generic-level classification on his findings, and proposed an evolutionary zoogeographic scenario for the radiation of the group. Vecchione *et al.* (in press) have used a phenetic analysis of loliginids as the basis of a generic-level taxonomy. Others, including Augustyn and Grant (1988) and Brierley and Thorpe (1994), have used allozyme electrophoresis to address problems of loliginid relationships. Despite such efforts, these authors admit that further work is necessary to clarify loliginid phylogeny.

No researchers have explicitly addressed loliginid phylogenetic relationships using cladistic methodology. Cladistic analysis allows many discrete character data to be considered simultaneously using an explicit, simple optimality criterion in which the preferred tree is the one which requires minimal assumptions of convergence and reversal across all characters in the analysis (the criterion of maximum parsimony) (Edwards and Cavalli-Sforza, 1964; Camin and Sokal, 1965; Kluge and Farris, 1969; Fitch, 1971; Farris, 1983; Sober, 1988; see Wiley *et al.*, 1991, for a review of cladistic philosophy and techniques). Cladistic analysis yields a hypothesis of phylogenetic relationships with which to interpret biogeographical patterns and character evolution (Brooks and McClennan, 1991; Maddison and Maddison, 1992). Phylogenetic hypotheses can also be used to construct taxonomic schemes (de Queiroz and Gauthier, 1990, 1992).

For this study, many aspects of loliginid morphology (particularly the hectocotylus, arm and tentacle-club sucker rings, spermatophores, fins, and some aspects of

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internal anatomy) were coded into a matrix for cladistic analysis to examine species-level relationships within the family. These data were analyzed using a maximum-parsimony algorithm program, and the results were compared with traditional taxonomic schemes and recent reclassifications. The strengths and problems of using morphological characteristics for examining loliginid evolution are addressed, and topics for future research are briefly outlined.

MATERIALS AND METHODS

DATA COLLECTION

Forty-eight morphological characters for 40 species of loliginid squids and eight outgroup taxa were coded into a data matrix in MacClade 3.04 (Maddison and Maddison, 1992) (Appendix I). Character states were determined through direct study of museum specimens at the National Museum of Natural History, the California Academy of Sciences, and the Invertebrate Museum at the University of Miami Rosenstiel School of Marine and Atmospheric Science, as well as published species descriptions (Appendix III). Some described loliginid species [including *Loligo arabica* (Ehrenberg, 1831) and newly described species such as *Photololigo robsoni* (Alexeyev, 1992)] were not included in this study because descriptions of these species were insufficient to code many characters with confidence, and specimens were not available for examination at the institutions I visited.

The outgroup method (Watrous and Wheeler, 1981; Maddison *et al.*, 1984) was used to polarize character transformations in this study. The eight outgroup taxa represent a broad range of decapod cephalopod diversity. Four oegopsid taxa (*Moroteuthis* Verrill, *Todarodes* Steenstrup, *Ctenopteryx* Appellöf, and *Bathyteuthis* Hoyle), two sepiolid taxa (*Euprymna* Steenstrup and *Rossia* Owen), and one sepiid taxon (*Sepia* Linné) were included, along with *Pickfordiateuthis pulchella* Voss, 1953. *Pickfordiateuthis* was originally described by Voss (1953) as a monospecific taxon closely related to Loliginidae as another member of the Myopsida. Recently, two new species of *Pickfordiateuthis* have been described, and *Pickfordiateuthis* has been subsumed within Loliginidae (Brakoniecki, 1996). For this analysis, *P. pulchella* was used as a representative of this group of squids. These outgroups were selected for a variety of reasons. In some cases, earlier authors have suggested that certain oegopsid taxa are close relatives of Loliginidae (*e. g. Ctenopteryx*; Young, 1991). In contrast, Berthold and Engeser (1987) suggested that Loliginidae, Sepiolidae, and Sepiidae are all closely related members of the Myopsida. Morphological similarities also exist between loliginids and various active nektonic oegopsids like *Todarodes*. Due to this uncertainty, a diversity of cephalopod taxa were included as outgroups in this study.

Many characters included in this analysis (such as hectocotylus morphology, sucker ring dentition, and fin shape) have been used in traditional studies of loliginid taxonomy, but have never been objectively analyzed simultaneously. In certain cases, some of these characters have been presumed to be informative at some taxonomic levels but not at others. For example, arm-sucker ring dentition generally has been used to distinguish between very similar species (Natsukari, 1983; Brakoniecki, 1986), but it has not been used as a taxonomic character above this level. In other cases, some characters have been examined only in those supraspecific taxa where they help unite or separate species (*e. g.* number of trabeculae per marginal club sucker in *Alloteuthis* Wülker; Hanlon *et al.*, 1992), and might not have been thoroughly examined in all loliginid species. Still other characters (*e. g.* spermatophore morphology) have been examined widely in loliginids, but have not figured importantly so far in cephalopod systematic studies (Hess, 1987; deMaintenon, 1990). Some characters were found to vary among loliginid species but were consistent within species, and were included in this analysis. Certain characters of traditional importance were avoided because they appeared to vary within certain species, and too few specimens were available to resolve these inconsistencies. For example, thickenings of the lateral edges of the vane of the gladius are for some authors important diagnostic characters for the genera *Doryteuthis* Naef and *Loligo* Lamarck but have been found to be variable within species (Cohen, 1976; Toll, 1982). Despite this, some polymorphic characters (characters that vary within some terminal taxa) were included in the analysis. Characters exhibiting intraspecific variation can contain strong phylogenetic signal (although generally not as strong as fixed characters) and thus should not be ignored or simply coded as fixed in cladistic analyses (Wiens, 1995). *A priori* assumptions about the information value of characters (other than inclusion of "traditional" well-studied characters in the analysis) were avoided, but inevitably (as in all phylogenetic studies) some characters that could be phylogenetically informative have been excluded. Appendix II lists the characters, argumentation and coding scheme used in this analysis.

Data for some characters are either not applicable for certain taxa ("n" in Appendix I) or could not be determined ("?" in Appendix I). Inapplicable characters usually refer to some aspect of a structure which is not present in all taxa in the analysis (*e. g.* "hectocotylus dorsal row sucker morphology" in taxa which do not possess hectocotyluses). In some cases, coding of "inapplicable" characters in this manner can cause problems in cladistic analyses (Maddison, 1993), but the solution advocated by Maddison

(1993) – combining all such characters into one character with many states – is often impractical and can lead to the loss of phylogenetic information. For example, in the case of this analysis, fusing all nine hectocotylus characters into one multistate character with many states was not performed. Fusing all hectocotylus characters into a single character with many distinct unordered states does not allow homology statements for individual aspects of hectocotylus morphology. It is possible, for instance, that species that possess a particular type of modified sucker, irrespective of the region of the arm that bears the modification, constitute a monophyletic group relative to species with other types of sucker modification, or vice versa. If the hectocotylus characters were fused into one unordered multistate character, this information would be lost – only species with almost exactly the same hectocotylus morphology (*i. e.* the same coded state for the single hectocotylus character) would be grouped together. Maddison's (1993) method is valid, but maximally conservative, and a great deal of phylogenetic information could be lost by collapsing characters in this way.

DATA ANALYSES

These data were analyzed using the maximum parsimony program PAUP 3.1.1 (Swofford, 1993). When terminal taxa were coded as having multiple states for one or more characters, these characters were interpreted as "polymorphic." All characters were unordered binary or multistate characters, and were weighted equally for all initial analyses. The use of equal weighting does not mean that each character in the matrix is of equal informative value. I have chosen to use equal weighting simply because I have no compelling reason to use any particular *a priori* differential weighting scheme (see discussion in Eernisse *et al.*, 1992). Heuristic searches were performed with 100 replications of random stepwise addition of taxa using tree bisection-reconnection swapping with one tree held at each step. The maximum number of trees stored for each search (MAXTREES) was 10,000. The COLLAPSE option was turned off for some analyses in an effort to find all regions of "islands" of most-parsimonious trees (Maddison, 1991; Swofford, 1993). Following Maddison's (1991) suggestion, a total of ten heuristic analyses were done to search for other islands and to examine the level of support for various branches within cladograms. A strict consensus cladogram was computed from the trees from each of the ten heuristic searches, for a total of ten strict consensus cladograms. A strict consensus of these ten strict consensus trees (a "grand strict" consensus cladogram) collapsed all ambiguities and revealed elements common to all trees from all ten searches.

After these preliminary analyses, two methods were used in an attempt to reduce tree number and investigate the phylogenetic utility of individual characters. The "reweight characters" option in PAUP was used to successively weight characters after each heuristic search (following the approach of Farris, 1969). Farris (1989) proposed the rescaled consistency index (RCI) and suggested its use in successive weighting analyses. In this analysis, characters were reweighted on the basis of their best rescaled consistency index value across the trees from the previous search. A heuristic search (following the same parameters as described above) was performed using the reweighted characters. Rounds of successive weighting were repeated until overall strict consensus tree topology did not change from one round to the next, or until character weights did not change after reweighting. As in preliminary analyses, strict consensus cladograms from the final round of weighting were combined, and a grand strict consensus cladogram was computed. This allowed common elements found in all successive weighting analyses to be determined.

A recently described technique called "safe taxonomic reduction" (Wilkinson, 1995) was also used in an effort to reduce the number of trees found. Analysis of matrices containing taxa with many missing data can result in an inordinately large number of equally parsimonious trees, because taxa with a large percentage of missing data (termed negatively underdetermined taxa) can occupy a number of equally parsimonious positions (Wilkinson, 1995). Consensus methods can be used to find common elements across multiple most-parsimonious trees (MPT's), but negatively underdetermined taxa can obfuscate patterns of relationship among other taxa that are found in all trees, yielding an extreme lack of resolution in strict consensus cladograms. The goal of safe taxonomic reduction is to remove negatively underdetermined taxa from the analysis without losing information about relationships (*i. e.* without altering patterns of relationships among the remaining taxa). This reduction in the number of negatively underdetermined taxa often reduces greatly the number of MPT's found by parsimony analysis. Increased resolution in consensus cladograms is often found after safe taxonomic reduction. In these analyses, the only taxa that could be safely removed from the ingroup using Wilkinson's technique were *Alloteuthis africana* and *A. media*, which were taxonomic equivalents of *A. subulata*, and *Loliolus affinis*, which was a taxonomic equivalent of *L. hardwickei*.

The phylogenetic signal of the data was evaluated using the g_1 test of Hillis and Huelsenbeck (1992). Based on simulation data, Hillis and Huelsenbeck (1992) proposed the use of the g_1 statistic (a measure of skewness) as one way to evaluate the ratio of signal to random noise in phylogenetic data. They found that high degrees of left-skew in plots of random tree distributions or total tree distributions obtained through exhaustive searches correlated well with the success of parsimony methods in finding the true phy-

logeny in simulation studies. Ten thousand random trees were generated based on this matrix using PAUP 3.1.1 with multistate taxa interpreted as polymorphic. The g_1 from this random tree distribution was compared to 95% and 99% confidence-limit values obtained from simulations with 50 binary or multistate characters and 25 taxa performed by Hillis and Huelsenbeck (1992), which should provide an approximate conservative comparison. In addition, all clades or sister-species groupings found across all trees (*i.e.* groupings retained in the grand strict consensus) were constrained to examine if phylogenetic signal was clustered within these groups. If the g_1 value (a negative value in left-skewed distributions) increases greatly after these constraints are applied, a large proportion of the phylogenetic signal in the matrix can be clumped within the universally supported clades, and is not evenly distributed across all data (Hillis and Huelsenbeck, 1992).

RESULTS

All unconstrained, unweighted analyses of all characters and all taxa resulted in 10,000+ most-parsimonious trees — the MAXTREES limit of 10,000 was reached in all analyses. The strict consensus cladogram of all sets of 10,000 trees from all ten unconstrained and unweighted heuristic searches is shown in Fig. 1. Tree lengths and statistics of the constituent trees are shown in Table 1.

The strict consensus cladogram of the ten final strict consensus trees from successive weighting was marginally more resolved than the strict consensus of the unweighted analyses (Fig. 2). Characters that were maximally and minimally weighted after multiple rounds of successive weighting are shown in Table 2.

Employing safe taxonomic reduction and removing *Alloteuthis africana, A. media,* and *Loliolus affinis* from the analyses had no apparent effect on the number of trees found in either unweighted or successive weighting analyses, or in the topology of the strict consensus cladograms from these analyses. Ten thousand trees were still found in all analyses following the removal of these taxa. The relative positions of *A. subulata* and *L. hardwickei* alone were the same as their positions when all taxa were included in the analysis.

Table 1. Tree statistics for 10,000 most-parsimonious trees found in the ten unweighted heuristic analyses.

Indices for unweighted trees
Consistency index (CI) = 0.582
Homoplasy index (HI) = 0.572,
Retention index (RI) = 0.663
Rescaled consistency index (RCI) = 0.386
Treelength (TL) = 194

Table 2. Maximally and minimally weighted characters across all weighted analyses (based on best rescaled consistency index fit). Characters that vary within the ingroup are denoted by an asterisk (*).

Maximally weighted characters	
Character Number	Description
1	rachidian cusps of radula
2	lateral cusps of radula
5	number of arm sucker rows
14	retractile tentacles
15	trabeculae number*
20	photophores on ink sac*
25	ventral row modification*
29	fused crest in ventral row of hectocotylus*
38	spermatophore placement*
40	spiral filament
43	pores on ink sac*
46	muscular septum
47	nuchal cartilage
48	digestive gland
Minimally weighted characters (weighted to zero)	
Character Number	Description
4	arm sucker rings
10	central manus sucker teeth*
13	marginal manus sucker teeth*
16	buccal membrane lobes
18	buccal lappet sucker teeth
19	buccal membrane formula
27	length of hectocotylus*

The g_1 skewness test of Hillis and Huelsenbeck (1992) suggests the presence of significant phylogenetic signal in the unweighted data matrix. The g_1 value for 100,000 random trees derived from this data matrix was -1.275647. This value was appreciably below the critical values for 50 binary or 50 four-state characters for 25 taxa [95% confidence limit for binary characters = -0.10, for four-state characters = -0.12; 99% confidence limit for binary characters = -0.11, for four-state characters = -0.13, based on simulation studies (Hillis and Huelsenbeck, 1992)]. When this procedure was repeated with the universally supported clades retained (using the grand strict consensus as a constraint), the g_1 value for a distribution of 100,000 random trees was -0.502625. This value suggests that even when universally supported clades are constrained, significant phylogenetic signal remains.

DISCUSSION

A small number of ingroup sister-species and subclade relationships were supported in the multiple

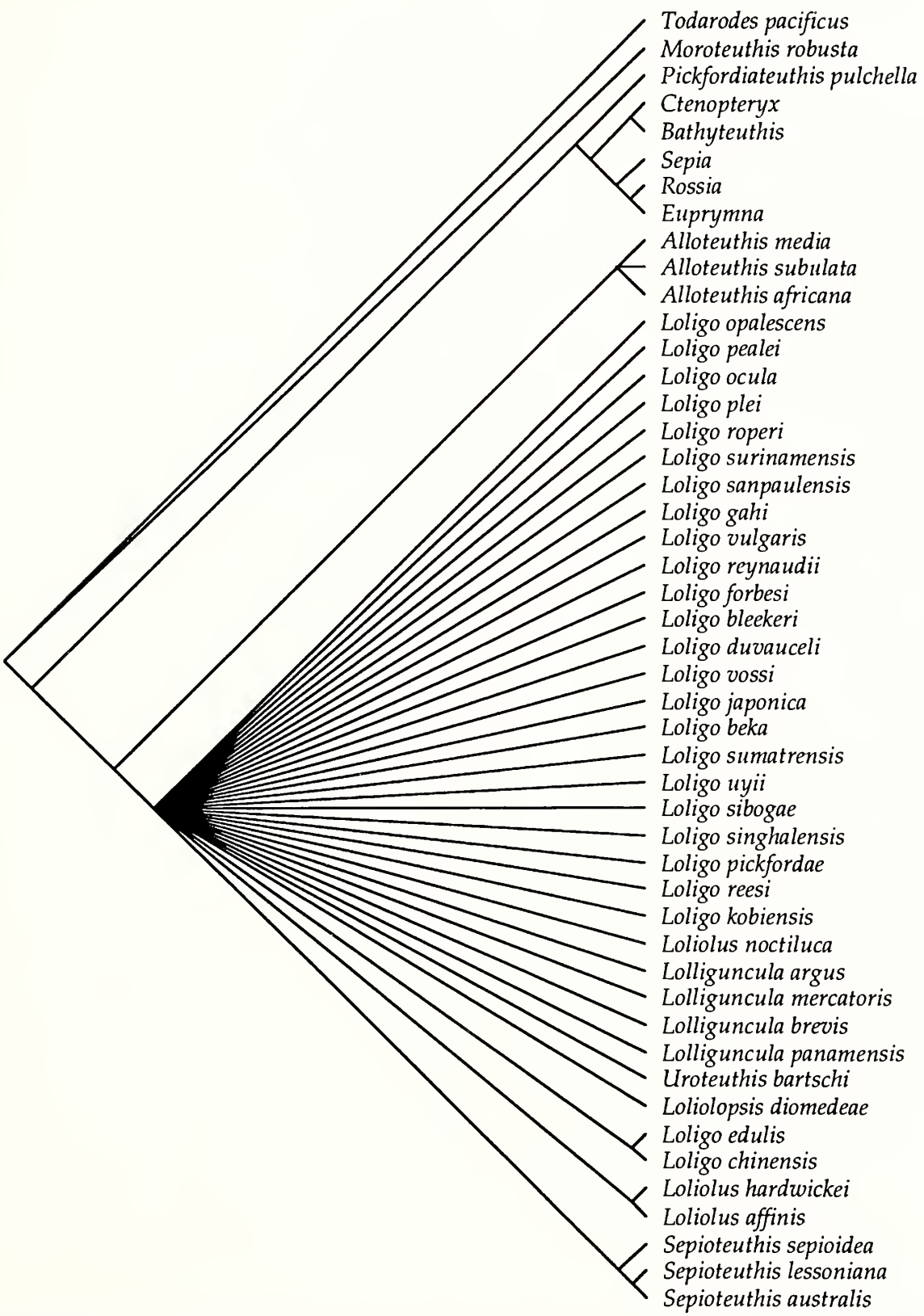

Fig. 1. Grand strict consensus cladogram of ten strict consensus cladograms derived from ten heuristic searches yielding 10,000 trees each. Tree statistics for the trees upon which this strict consensus is based are shown in Table 1.

unweighted heuristic analyses (Fig. 1), but deeper branching orders and relationships among loliginid squids remain unresolved, despite the relatively high phylogenetic signal suggested by the g_1 test. Successive weighting analyses consistently suggested support for some higher-level relationships (Fig. 2), but even with successive weighting and safe taxonomic reduction, tens of thousands of most-parsimonious trees were found, and, despite some interesting findings, the resulting grand strict consensus cladograms are largely unresolved.

Monophyly of Loliginidae was supported by all unweighted and weighted analyses. Myopsida (traditionally comprised of Loliginidae + Pickfordiateuthidae) was found to be paraphyletic in all unweighted and weighted analyses. Brakoniecki's (1996) inclusion of *Pickfordiateuthis* within Loliginidae is not justified based on these analyses. Within the ingroup, only four clades were consistently supported in all unweighted analyses, and two of these are sister-species groupings. Monophyly of the genus *Alloteuthis*, consisting of three species of small, slender squids found in the eastern Atlantic along the coasts of Europe and Africa (*A. africana, A. media,* and *A. subulata*) was supported in all analyses, and was the sister taxon to the rest of Loliginidae. *Alloteuthis* appears to have diverged from the other loliginid species early in the history of the group. Monophyly of the genus *Sepioteuthis* Blainville, which is comprised of *S. australis* and *S. lessoniana* (both Indo-West Pacific species), and *S. sepioidea* (a Caribbean species) was also supported in all unweighted analyses. Two synapomorphies appear to unite the three species of *Sepioteuthis* – a longitudinally oval fin shape uniquely derived within Loliginidae, and the large size of the dorsal row of papillae relative to the ventral row in the modified portion of the hectocotylus. In addition to these three-taxon clades, two sister-species pairings were consistently found – *Loligo chinensis* and *L. edulis* in one pairing, *Loliolus hardwickei* and *L. affinis* in the other. All other relationships within Loliginidae are unresolved in the unweighted analyses.

There are a number of possible explanations for this lack of resolution. First, the number of characters employed (48) is relatively low compared to the number of terminal taxa (48) included in the analysis. Another important factor might be that many of the characters used in the analysis are highly homoplastic, showing evidence of multiple convergences or reversals throughout the evolution of this group. Several of the characters included in this analysis have been used extensively in decapod cephalopod taxonomic studies, and appear to be very useful for distinguishing species, but when relationships among all loliginid species are studied and characters are atomized for cladistic analysis, individual characters can exhibit high levels of homoplasy.

Successive weighting techniques have been used by many authors to reduce the number of most-parsimonious trees, to increase resolution in consensus trees, as a heuristic tool to investigate the cladistic informativeness of characters, and to study the effect of homoplastic characters in cladistic analyses (Farris, 1969; Carpenter, 1988, 1994), but some authors have criticized the use of successive weighting techniques (Swofford and Olsen, 1990) or have urged caution in the interpretation of results from successive weighting analyses (Maddison and Maddison, 1992; Swofford, 1993; Suter, 1994). Some investigators (*e. g.* Suter, 1994) have found that the parameters used in successive weighting analyses can have an effect on the outcome of successive weighting analyses. In addition, successive weighting does not necessarily reduce the number of most-parsimonious trees – in this analysis, the tree buffer limit was reached on all analyses, unweighted or weighted. Successive weighting can reduce the weight of highly homoplastic characters to zero, effectively removing them from the analysis [seven characters were weighted to zero by the final round of weighting in these analyses (Table 2)]. As the number of characters actually included in the analysis drops, resolution in strict consensus cladograms likely will drop, particularly when the number of characters is small relative to the number of taxa in the analysis.

Farris (1969) and Carpenter (1988, 1994) have strongly supported successive weighting as simply an extension of the concept of cladistic reliability, or the degree of fit between a character and the phylogeny (Farris, 1969). Successive weighting allows *a posteriori* weighting based on the cladistic information value of the characters in the matrix. Characters that show little homoplasy when evaluated in conjunction with all other characters in the matrix are increased in weight (or set at a maximum base weight in PAUP 3.1.1) relative to characters exhibiting more homoplasy in subsequent rounds of analysis, while highly homoplastic characters are reduced in relative weight. Carpenter (1988, 1994) has argued that successive weighting "allows the characters of a given data set to judge themselves in terms of their reliability; that is, best fit to the solution supported by all the characters" (Carpenter, 1994: 216).

Successive weighting analyses supported all clades found in earlier, unweighted analyses, and suggested three other groupings not found in unweighted analyses. Two major clades were supported in all final weighted analyses – a clade consisting of all loliginid species possessing paired bioluminescent organs on the ink sac [*Loligo edulis, L. chinensis, L. duvauceli, L. sibogae, L. singhalensis, L. pickfordae* (Adam, 1954), *L. reesi, Loliolus noctiluca,* and *Uroteuthis bartschi*, all found in the Indo-West Pacific], and a clade consisting of seven other Indo-West Pacific species (*Loligo beka, L. japonica, L. sumatrensis, L. uyii, L. kobiensis, Loliolus hardwickei,* and *L. affinis*). In addition,

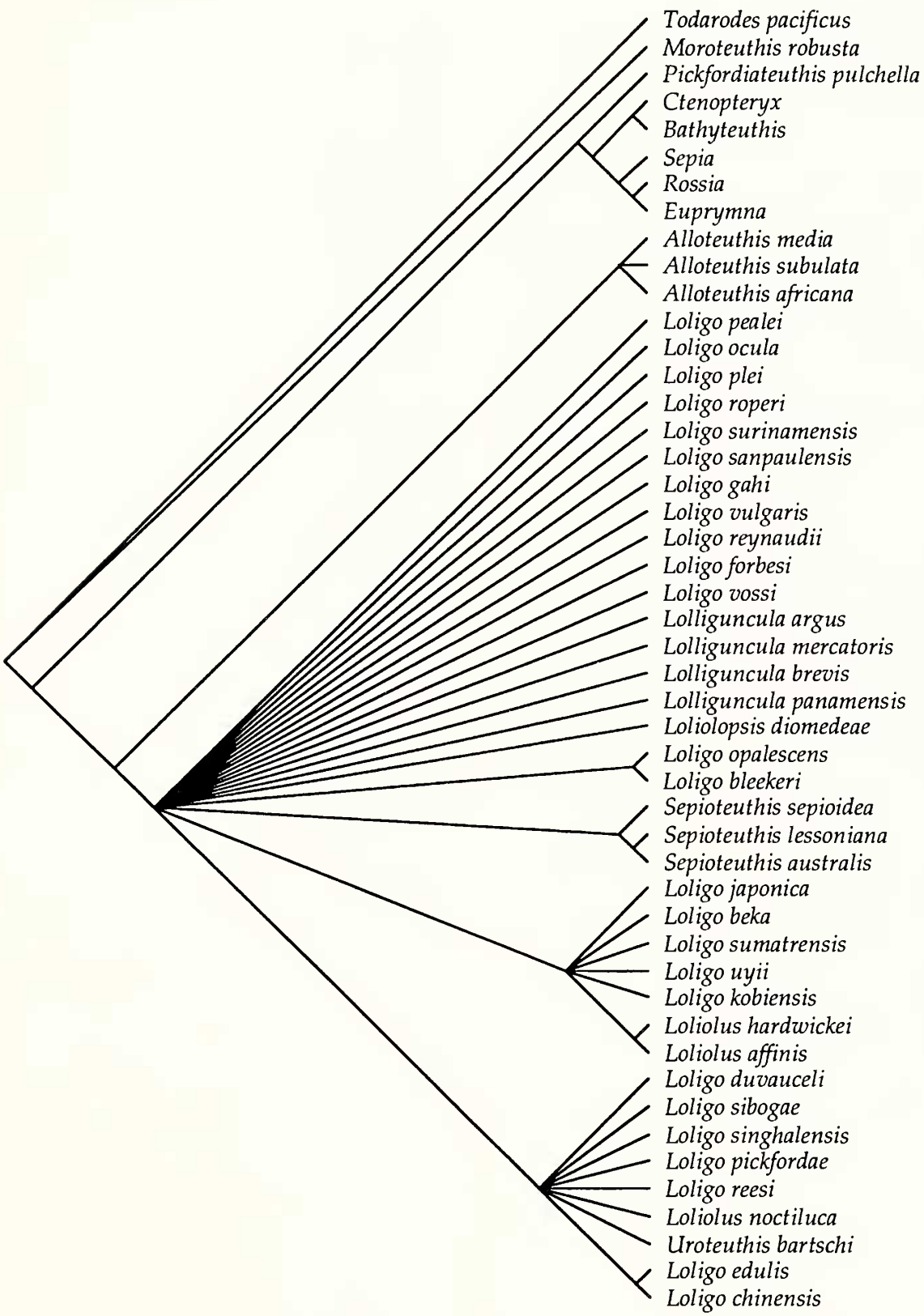

Fig. 2. Grand strict consensus cladogram of ten strict consensus cladograms from successive weighting analyses from each of ten heuristic searches.

Loligo opalescens and *L. bleekeri* were found to be sister species in all final weighted analyses.

The major putative synapomorphy uniting the bioluminescent loliginids are the paired bean-shaped bacterial photophores (luminescent organs) on the ventral side of the ink sac. This clade is similar to the proposed genus *Photololigo* Natsukari (1984), which includes five of these species (*Loligo edulis, L. duvauceli, L. chinensis, L. singhalensis,* and *L. sibogae*) as well as *L. arabica*, which was not included in this analysis. Natsukari's *Photololigo*, however, does not include *L. reesi, L. pickfordae, Loliolus noctiluca,* or *Uroteuthis bartschi*. Results of this weighted analysis support Vecchione *et al.*'s (in press) *Photololigo* as a monophyletic group. However, these authors divide *Photololigo* into two smaller groups – a subgenus *Photololigo* and a subgenus *Uroteuthis* (consisting only of one species – *U. bartschi*). It is possible that *U. bartschi* is a derived member of the photololiginid clade. If this is true, Vecchione *et al.*'s (in press) subgenus *Photololigo* is paraphyletic with respect to their subgenus *Uroteuthis*. Unfortunately, cladistic analysis of these data cannot address this question. Alexeyev (1992) has reported that some specimens of *Lolliguncula mercatoris* and a single specimen of *Loligo forbesi* appeared to possess photophores on the ink sac. In this analysis, these species are considered to lack photophores, pending further investigation (as suggested by Vecchione *et al.*, in press). If Alexeyev's (1992) findings are accurate, they must be accounted for in future phylogenetic studies of this group.

More detailed studies of the primary synapomorphy that unites the species of *Photololigo* – the photophores themselves – might help resolve these problems. In *Euprymna*, the bioluminescent organ is the product of a complex interaction between the squid and symbiotic luminescent bacteria (McFall and Ruby, 1991). Further investigations of this interaction and its effects on photophore morphology in all photololiginid squids (*e. g.* Haneda, 1963; Pringennies and Jørgensen, 1994) could illuminate species relationships within the clade.

The other major clade found in the weighted analyses is very similar to Natsukari's (1983) *Nipponololigo*, a proposed subgenus of *Loligo* comprised of *L. japonica, L. uyii, L. kobiensis,* and *L. beka*. The successive weighting analyses support the inclusion of *L. sumatrensis* and the *Loliolus affinis-hardwickei* sister-species grouping within a broader *Nipponololigo* clade. The two synapomorphies uniting these species are the sucker morphology of the dorsal and ventral rows of the hectocotylus. The pedicels of the dorsal row suckers are fused with their protective membrane and widened into fleshly slabs (Natsukari, 1983; Brakoniecki, 1986). In most of these species, the slabs retain small suckers; in *L. affinis* and *L. hardwickei*, however, the suckers are not present on the tops of the slabs. In these analyses, the lack of suckers on the tops of the slabs was revealed as a synapomorphy uniting these two species as sister taxa. In the ventral row of the hectocotylus, all species in the *Nipponololigo* clade possess minute, apparently suckerless papillae. Vecchione *et al.* (in press) have proposed the name *Loliolus* to include all members of Natsukari's *Nipponololigo* as well as *L. affinis* and *L. hardwickei*. These species are divided into two subgenera – *Loliolus (Loliolus)* (comprised of *L. affinis* and *L. hardwickei*) and *Loliolus (Nipponololigo)* (comprised of the species in Natsukari's *Nipponololigo*, plus *L. sumatrensis*). As with *Photololigo,* these analyses generally support their conclusion, although a paraphyletic *Nipponololigo* (with respect to *L. affinis* and *L. hardwickei*) is a possibility that cannot be addressed with these data alone.

Loligo opalescens and *L. bleekeri* constitute a sister-species pairing in all weighted analyses. Brakoniecki (1986) anticipated this result. He proposed that the epithet *Doryteuthis* (subgenus *Doryteuthis*) be applied to six species of loliginid squids. Five of these species (*Loligo plei, L. roperi, L. sanpaulensis, L. gahi,* and *L. opalescens*) are found in American waters, while one species (*L. bleekeri*) is found only in Japanese waters. *Doryteuthis (Doryteuthis)* and *Sepioteuthis* are the only geographically disjunct groupings described by Brakoniecki (1986). Brakoniecki proposed a causal explanation for the distribution of *Doryteuthis (Doryteuthis)* – he suggested that a slight rise in water temperature in the northern Pacific Ocean could have allowed the *L. bleekeri-opalescens* common ancestor to disperse from the eastern Pacific coast of North America to Japan via the Aleutians. The results of the weighted analyses support a sister-species relationship between *L. bleekeri* and *L. opalescens*, but, due to the lack of resolution of relationships among other *Doryteuthis (Doryteuthis)* species, a monophyletic subgenus *Doryteuthis* (*sensu* Brakoniecki, 1986) remains a possibility, but is not directly supported. Due to the overall lack of resolution, the possible ancestral range of the *L. bleekeri-opalescens* ancestor cannot be examined.

In addition to these putative clades, certain species presently grouped in the genus *Lolliguncula* (*L. panamensis, L. mercatoris,* and *L. brevis*), together with *Loliolopsis diomedeae*, were found in all strict consensus trees from all weighted analyses. However, the position of *Lolliguncula argus* was variable across these trees. In some consensus trees, *L. argus* was completely outside the clade comprised of the rest of the *Lolliguncula* species plus *Loliolopsis diomedeae*. In other trees, *L. argus* was found to be a highly derived member of the *Lolliguncula* + *Loliolopsis* clade. Due to the variable position of this taxon, the *Lolliguncula* + *Loliolopsis* clade collapsed in the overall strict consensus cladogram (Fig. 2).

Successive weighting analyses can provide heuristic

insight into the information value of the characters in the analysis. Most informative, consistent characters found after multiple rounds of successive weighting are invariant within the ingroup (Table 2). Few characters that vary within the ingroup appear to have high rescaled consistency indices across all initial unweighted trees. Also, several characters show varying amounts of homoplasy across initial unweighted most-parsimonious trees, and subsequently have low weights after successive weighting analyses.

The overall lack of resolution in strict consensus trees found after these unweighted and weighted analyses and the low weights of many characters after successive weighting highlight the limited utility of using only gross external morphological characters to investigate loliginid squid phylogeny. Despite this general conclusion, external morphological characters should not be ignored in future investigations of loliginid relationships. The Hillis and Huelsenbeck (1992) g_1 test shows significant phylogenetic structure in the data matrix. Some of the characters used in this analysis do appear to carry appreciable phylogenetic information. Undoubtedly, more data must be gathered to test the results of these analyses and to resolve relationships among these squids. Little is known about comparative internal anatomy in loliginid squids, although excellent studies have been done of particular species (*e.g.* Williams, 1909). For example, the anatomy of the nervous system and circulatory system, and perhaps aspects of juvenile development, are particularly promising systems for inclusion in cladistic analysis. Many neurophysiological studies have been performed on a broad range of loliginid squids, including *Loligo opalescens, L. pealei, L. vulgaris, Sepioteuthis lessoniana, Lolliguncula brevis,* and *Alloteuthis media* (*e.g.* Brown *et al.*, 1991; Chrachri and Williamson, 1993; Fishman and Metuzals, 1993; Preuss and Budelmann, 1995). Due to the ease of culturing some of these species in the laboratory (Lee *et al.*, 1994), and the giant axons of many loliginids, more comparative neurological studies undoubtedly will be performed. These data could be combined with other morphological and anatomical data for cladistic analysis.

In addition to internal anatomical information, molecular data could aid in resolving loliginid relationships. Recently, Yeatman and Benzie (1994) have found genetic evidence of cryptic speciation within *Photololigo edulis* and *P. chinensis*, providing evidence of the power of molecular techniques in species-level research of loliginid squids. An ongoing sequencing study of two mitochondrial genes (the 16S ribosomal DNA gene and the cytochrome *c* oxidase subunit I gene) could shed light on loliginid relationships (Anderson, unpub.). Relationships among loliginid squids at the species level and investigations of cladogenesis and biogeography within this group will be possible only through an examination of multiple sources of data, including morphological, anatomical, and molecular sequence data.

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APPENDIX 1 - Data Matrix. Inapplicable characters for particular taxa are indicated by "n", while missing or unknown character states are coded as "?". Certain taxa are polymorphic for particular characters. In these cases, the following code was used: "a" = states 0 and 1, "b" = states 1 and 2, "c" = states 0 and 2, and "d" = states 1 and 3. Taxon names above the species level are based on Nesis (1987).

	1111111111222222222233333333334444444444 1234567890123456789012345678901234567890123456789012345678
Todarodes pacificus	11?10102011010100n103nnnnnnnn2000????????2000010
Rossia	00?1a??0?110?1?20n001nnnnnnnn0111????????0011101
Moroteuthis robusta	11?00nn3?2???0??0n000nnnnnnnn2000?????2002?00010
Sepia	00?01nn200??01?01?002nnnnnnnn1nn10???????n011011
Ctenopteryx	???11??0nnnnn0??1?010nnnnnnnn3nn1?????20?0?00010
Bathyteuthis	00?11110nnnnn0?011100nnnnnnnn0110?????20?0?00010
Euprymna	00?0ann0nnnnn1?10?021nnnnnnnn01100??????0011101
Pickfordiateuthis pulchella	110a0?31?0???0?20?0021266?00?01110001?1000?11010
Loligo opalescens	11?10112011 0a0001100202 00?00?20010000a???0011010
Loligo pealei	11110112011110?0110021200?01?2001?000a0110011010
Loligo ocula	11?10112?11110?01?0021210?01?2001?0000???0?11010
Loligo plei	11110112011110?0110020110?01?2001100000110011010
Loligo roperi	11?10112011010?01?0020210?01?2001000000110011010
Loligo surinamensis	11?10112011110?01?0021210?00?2001?00000110?11010
Loligo sanpaulensis	11?10122011010001000 2001??01?2001?0000?100?11010
Loligo gahi	11?10112011010001000 2001??01?2001100000110011010
Loligo vulgaris	11?10112010 0?0?0110020111?00?2001100 0????011010
Loligo reynaudii	11?10a12?a1010?01?00201bb?00?2001?0000011??11010
Loligo forbesi	11?10132?110?0?0110020111?01?2001?0000?????11010
Loligo bleekeri	11?10???2?????0?01?0020100?00?2001100 0?????11010
Loligo duvauceli	11?10112111010001?03201111 0 0?2001?2200?1?0011010
Loligo edulis	11?10112111110001003201221 0 0?2001122 0 0?1??011010
Loligo chinensis	11?10102111110?0110320122000?2001011 0 0?1??011010
Loligo vossi	11?10012011010?01?0020111 10??2001 1????????11010
Loligo japonica	11?10112011010001?0020154?0012001?1100????011010
Loligo beka	11?101b2011010?01?0020154?0012001?1100?1???11010
Loligo sumatrensis	11?10112010010?01?0020154?0??2001 0000??1??011010
Loligo uyii	11?10122 0??10001?0020154?0012001?1100?????11010
Loligo sibogae	11?10112111 0?0001?03201221 0 0?2001 1???0?1??011010
Loligo singhalensis	11?101a2111110?01?03201111 0 0?2001?00001100011010
Loligo pickfordae	11?10012?110?0?01?03201??????20011????????011010
Loligo reesi	11?10112111010?01?0320111?10?2001 000?0110011010
Loligo kobiensis	11?1012200??10001?0020154?0012001?02100110011010
Alloteuthis media	11?1011201aa10100n00201bb100?212100010???1011010
Alloteuthis subulata	11?1011201aa10100n00201bb100?2121000100111011010
Alloteuthis africana	11110112011 0?0100n00201bb100?212100010???1011010
Loliolus hardwickei	11010122110010001100 2354?0002101022?02110111010
Loliolus affinis	11?10122110 0?0001?0022354?c0021010???0?110111010
Loliolus noctiluca	11?1011200??0000100322311?10?21010???01110011010
Sepioteuthis sepioidea	11010112110010000n0020111200?1nn100020???0011010
Sepioteuthis lessoniana	11?10002111010001100201112 00?1nn1000001110011010
Sepioteuthis australis	11?10002111010001100201112?0?1nn10000001 1?011010
Lolliguncula argus	11?10112011 0?0?00n00300d??a0?211101003010 0011010
Lolliguncula mercatoris	11?10022?110?0?00n00201333 01?211102202?????11010
Lolliguncula brevis	11?10122111010001?0020a3a?a0?2111000010100011010
Lolliguncula panamensis	11?10122111aa00011002003??10?2111000020100011010
Uroteuthis bartschi	11210112111 0?0001?03201010 00?2021100000111011010
Loliolopsis diomedeae	11110112011 0?0?01?0020135?10?211100001???0011010

APPENDIX II. Character Descriptions and Codings. Supplemental sources of information used are listed by each character (or each character suite) with the exception of particular references that pertain to certain taxa, including: *Bathyteuthis* (Roper, 1969); *Pickfordiateuthis pulchella* (see Voss, 1953; Brakoniecki, 1996); *Alloteuthis africana* (see Adam, 1950) *Loligo pealei, L. ocula, L. plei,* and *L. roperi* (see Cohen, 1976); *L. sanpaulensis* and *L. gahi* (see Brakoniecki, 1984); *L. chinensis* (see Natsukari and Okutani, 1975; Nateewathana, 1992); *L. edulis, L. beka, Loliolus affinis, Loligo sumatrensis* (see Nateewathana, 1992); *L. surinamensis* (see Voss, 1974); *L. kobiensis/Loliolus rhomboidalis* (see Burgess, 1967); *Loligo sibogae* (see Adam, 1954; Natsukari, 1976); *L. pickfordae, L. duvauceli, L. singhalensis* (see Adam, 1954); *Loliolus* (Lu *et al.,* 1985); *Sepioteuthis* (Lu and Tait, 1983); *Lolliguncula argus* (see Brakoniecki and Roper, 1985); *L. panamensis* (see Berry, 1911; Brakoniecki, 1980); *Uroteuthis bartschi* (see Adam, 1954; Rehder, 1945; Voss, 1963), and *Loliolopsis diomedeae* (see Berry, 1929). Characters are grouped by system; numbers refer to the position of the character in the data matrix (Appendix I).

A. Radula

1. Rachidian tooth (unicuspid/tricuspid) - Within most squids, the radula is comprised of seven longitudinal rows of teeth – a central rachidian, a pair of first and second lateral teeth, and a pair of marginal teeth. The rachidian tooth is usually either composed of a single cusp (unicuspid), or has a large central tooth with two lateral cusps (tricuspid).
2. Lateral teeth (unicuspid/bicuspid) - The first and second lateral teeth within loliginids are comprised of two cusps, while the first and second lateral teeth in numerous other squids are unicuspid.

B. Arm/tentacle club/sucker rings

3. Brachial cartilage (absent/fibrous type/hyaline type) (deMaintenon, 1990) - The brachial cartilage is a small cartilaginous structure found in many squids located antero-ventrally to the cranial cartilaginous body. The brachial cartilage seems to serve as a base for the tentacles and fourth arms. Some loliginids (*e.g. Sepioteuthis sepioidea*) lack this structure altogether, some have either a variable region of fibrous connective tissue (coded as "fibrous type"), and still others possess a distinct block of hyaline cartilage ("hyaline type").
4. Arm sucker rings (smooth/with teeth) - All taxa in this analysis possess horny chitinous rings in their arm suckers. These rings are either smooth, or they possess teeth of various shapes.
5. Arm sucker rows (two/four) - All loliginids and many other squids possess two rows of stalked suckers running along the arms. Many cephalopods possess four rows of suckers along the inner surface of the arms.
6. Arm sucker teeth position (all around ring/only on distal edge) - In most loliginids, the teeth on the chitinous sucker rings of the large proximal suckers on the third and fourth arms are found only on the distal edge of the sucker rings. In particular species, the sucker ring teeth are found all around the ring (although decreasing in size in the proximal region of the ring).
7. Arm sucker teeth shape (sharp/square or rounded and blunt/low, wide and flat/small, low and rounded) - A great diversity of arm sucker tooth shape can be found among loliginid species. Teeth are generally either tall, slender, and sharply pointed (as in *Loligo chinensis*), tall with rounded tips, or relatively flat and wide (often considerably wider than tall). Some (such as *L. japonica*) possess low rounded teeth, usually slightly wider than tall, with rounded, half-circle edges. The lone specimen of *L. forbesi* examined possessed a unique tooth morphology, consisting of very small, irregular teeth, giving the ring a pebbly appearance.
8. Club morphology (many tiny suckers/two rows in manus/four rows in manus/no marginal suckers or distinct dactylus) - The number of sucker rows in the manus region of the tentacle clubs is variable among squids. Many taxa (such as *Bathyteuthis*) possess a large number of minuscule suckers on the tentacle clubs, with no distinct regions. Other squids possess a distinct carpus, manus and dactylus, with two rows of suckers in the manus region. All loliginid squids possess a distinct manus and dactylus, with four rows of suckers (two central rows and two outer marginal rows) in the manus. *Pickfordiateuthis* possesses a few large, central suckers in the manus, with no marginal suckers and no distinct dactylus.
9. Central club sucker size (much larger than marginal suckers/similar in size to marginal suckers) - There is substantial variation in the size of the central club suckers relative to that of the marginal club suckers. In some loliginid species, marginal club suckers are nearly as large as central suckers while, in others, the marginal suckers are considerably smaller than the nearby central suckers.
10. Central manus sucker teeth (absent/present/hooks) - Some loliginid species possess smooth, toothless chitinous rings in their largest central club suckers. Most loliginids have teeth of some kind on their central manus sucker rings. Some outgroup taxa possess sharp hooks in their club suckers.
11. Central manus sucker teeth shape (blunt/pointed) - Central club sucker teeth are generally sharp and pointed, but some species have central manus suckers with teeth with rounded or blunt tips.
12. Central manus sucker teeth pattern (uniform sizes/many with alternating small and large teeth) - Patterns in central club sucker teeth sizes are variable, even among suckers on one tentacle club. In general, however, teeth are subequal in size on each individual ring. In some species, teeth show an alternating pattern (often large-small-large-small). Some species show more complex patterns of alternating small, medium and large teeth.
13. Marginal manus sucker teeth shape (blunt/pointed).
14. Retractile tentacles (absent/present).
15. Trabeculae number per marginal club sucker (one per marginal sucker/two per marginal sucker) - Most loliginid species possess thick trabeculae (muscular supports for the protective membranes of the tentacle clubs) spaced evenly between the marginal club suckers, averaging one trabecula per marginal sucker. Other species (members of the genus *Alloteuthis*) possess two trabeculae (Roper *et al.*, 1984) attached near the base of each marginal sucker.

C. Buccal lappets

16. Buccal lappet lobes (seven/eight/no lobes) - The number of buccal lappet lobes is variable among squids, and has been used as a taxonomic character. All loliginid squids possess seven buccal lappet lobes.
17. Buccal lappet suckers (absent/present) - Most loliginid species have tiny suckers on the inner surface of their buccal lappets. The three species of *Alloteuthis* and *Sepioteuthis sepioidea* do not have suckers on their buccal lappets.
18. Buccal lappet sucker teeth (absent/present).
19. Buccal membrane formula (DDVV/DDVD) - The location of the buccal lappet supports relative to the arms has commonly been used in cephalopod systematic studies. In loliginids and many other squid groups, the buccal lappet supports are attached to the

dorsal edges of the first and second arms, and to the ventral edges of the third and fourth arms (this pattern is often abbreviated "DDVV"). In other squids, the supports are attached to the dorsal edge of the first, second and fourth arms, and to the ventral edges of the third arms (abbreviated "DDVD").

D. Photophore morphology

20. Photophores on ink sac (absent/one round photophore/one U-shaped photophore/two bean-shaped photophores) - Photophores (bioluminescent organs) of various types are widespread throughout many cephalopod taxa. Most taxa examined in this study lack photophores. Some (*Ctenopteryx*) possess a single large round photophore on the ink sac. Others (*Euprymna*) possess a large U-shaped photophore on the ventral surface of the ink sac. Some loliginid species possess two oval or bean-shaped photophores. These species have been grouped in three separate genera (*Loligo, Uroteuthis,* and *Loliolus*) by earlier authors, while recent workers have suggested that loliginids with photophores constitute a natural group (named *Photololigo*). Because photophore shape and number varies across Loliginidae, *Ctenopteryx,* and *Euprymna*, these structures have been coded as different states. Because photophore number and basic external morphology is similar across all loliginid species with photophores, these structures have been coded as putative homologues for this analysis. Only through cladistic analysis of many characters can individual statements of homology such as this be assessed (the test of congruence; Patterson, 1982).

E. Hectocotylus morphology (Brakoniecki, 1986)

21. Hectocotylized arms (none/left dorsal arm/left ventral arm/right ventral arm) - The hectocotylus is a modified arm (or arms) in males that aids in transfer of spermatophores to the female. Hectocotyluses can exhibit radically different sucker morphology from the other arms, or can be of a very different length from the rest of the arms. Different cephalopod taxa have different arms hectocotylized, or lack an obvious hectocotylus altogether.
22. Modified region in dorsal row of hectocotylus (distal suckers modified to tip of arm/central suckers only modified/all suckers modified) - The region of modified suckers in the dorsal row of the hectocotylus is variable across loliginid species. In most species, only the distalmost suckers show any sort of modification, extending to the tip of the arm. A few species (*Loliolus*) show sucker modification along the entire length of the arm. Other species show minimal sucker differentiation on the hectocotylus which is restricted to a central region of the arm.
23. Modified region in ventral row of hectocotylus (distal suckers modified to tip of arm/central suckers only modified/all suckers modified) - See description for character 22.
24. Type of sucker morphology in dorsal row (small suckers with large pedicels/tiny suckers with long triangular pedicel/robust conical suckerless papillae/long thin suckerless papillae/tiny papillae/small suckers and stalks) - Sucker modifications are extremely variable in loliginid hectocotyluses, but seem to fit into a few distinct classes, which may be related to one another in complex ways. Some hectocotyluses possess small suckers at the tip of large, thick, columnar stalks (pedicels). Others show a similar modification - tiny suckers at the tip of pedicels which are distinctly wider at the base than at the tip, giving them a triangular shape. Some species possess thick, conical "papillae" that appear to lack suckers of any kind, but come to a point at their tips. Others possess a similar, but distinct, sucker modification in which long, rounded finger-like papillae are found. Some species possess only minute papillae in the dorsal row of the hectocotylus. Finally, a few species have suckers that are slightly smaller than normal, but are otherwise unmodified.
25. Type of sucker morphology in ventral row (small suckers with large pedicel/tiny suckers with long triangular pedicel/robust conical suckerless papillae/long thin suckerless papillae/fused crest/no suckers/suckers embedded in swelling) - Most sucker modifications found in the dorsal row of the hectocotylus are also found in the ventral row. There are a few differences. In many species, the ventral row of suckers is present as a row of tiny papillae, similar in morphology to the "finger-like" papillae described above, but much smaller. In some species, the pedicels of the ventral sucker row are fused with the ventral protective membrane, resulting in a series of thickened slabs (a fused crest) in the ventral row. One species (*Loliolopsis diomedeae*) completely lacks suckers of any kind in the ventral row. The ventral row of suckers in *Pickfordiateuthis* appears to be embedded in a swelling, an autapomorphy of this taxon.
26. Size of suckers on hectocotylus (suckers of both rows about the same size/ventral row suckers larger/dorsal row suckers larger/dorsal row suckers larger proximally, ventral row suckers larger distally) - In many cases where the sucker modifications in both rows are the same, consistent differences in sucker height can be seen between the rows. In some cases, the suckers in each row are approximately equal in size, tapering to the tip of the arm. Alternatively, the suckers in either the dorsal or ventral row can be larger than adjacent suckers in the other row. In a few species, dorsal row suckers appear to be larger proximally, but rapidly decrease in size down the length of the arm, while suckers in the ventral row either increase in size, or decrease much more slowly, resulting in the dorsal row of suckers being larger proximally, but the ventral rows of suckers being larger distally.
27. Length of hectocotylus (same length as fellow arm/longer than fellow arm/shorter than fellow arm) - In most cases, the length of the hectocotylized ventral arm is approximately the same as the length of the non-hectocotylized ventral arm. In some cases, however, the hectocotylized arm is distinctly longer or shorter than the other ventral arm.
28. Ridge between sucker rows in modified region of hectocotylus (absent/present) - A fleshy ridge is evident between the sucker rows in the modified portion of the hectocotylus in some loliginid species. This ridge is lacking in males of most loliginid species.
29. Fused crest in ventral row (without suckers/with suckers) - In squids with a fused crest ventral row modification, some species have suckers at the tops of the crest, while others (*Loliolus hardwickei, L. affinis*) have a suckerless fused crest.

F. Fin morphology

30. General fin shape (subterminal and round/terminal, longitudinally oval/terminal, rhomboid, or transversely oval/longitudinally oval and trabeculate) - The general shape of the swimming fins on the mantle of cephalopods is highly variable. Fin morphology for the species in this study can be split into four groups. Some outgroup species possess small, round, or kidney-shaped subterminal fins. Some species (*Sepia, Sepioteuthis*) possess fins which extend from almost the anterior edge of the mantle to the posterior tip, and are shaped like half-ovals. *Ctenopteryx* possesses longitudinally oval, trabeculate fins that are rather distinct from the fins of other squids. Most loliginid species have terminal fins whose anterior attachment point is far from the anterior edge of the mantle. These fins are either rhomboid or transversely oval in shape.
31. Anterior fin edge (nearly straight/convex).

32. Posterior fin edge (straight/convex/concave, longer than anterior edge).

G. Sexual morphology

33. Accessory nidamental glands (absent/present).
34. Cutaneous ridge on ventral surface of mantle in males (absent/present) - Mature males of some loliginid species possess a robust, serrated ridge running the length of the ventral midline of the mantle. Males of most loliginid species lack this feature.
35. Male arm II sucker size (normal/proximal suckers enlarged/all suckers enlarged) - Males of particular loliginid species have larger suckers (either proximally, or along the entire length of the arm) on their second (dorsolateral) arm pair than females of similar size of the same species.
36. Male arm III sucker size (normal/proximal suckers enlarged/all suckers enlarged) - See description for character 35.
37. Male right arm IV sucker size (normal/proximal suckers enlarged/proximal suckers reduced) - As described in character 35, males of some loliginid species show enlargement (or reduction) of the proximal suckers of the right arm IV suckers relative to the proximal suckers on the hectocotylus (left arm IV).

H. Spermatophores (Hess, 1987)

38. Spermatophore placement (onto buccal membrane/near left gill on mantle wall/on buccal membrane and left gill/on buccal membrane and right gill) - Clusters of deposited spermatophores can often be found during dissections of females. The location of these clusters varies across species. Females in most species possess a spermatophore receptacle on the buccal membrane near the mouth. In some well-studied species, however, spermatophores have been found attached to the buccal receptacle and to the base of either the left or right gill. In particular species, toughened "spermatophoric pads" can be found on the inside of the mantle cavity near the left gill where spermatophores are attached. Lu *et al.* (1985) reported that some females of *Loliolus noctiluca* also possess spermatophoric pads, and other authors have seen spermatophores placed on the left side of the inner mantle wall in *Loligo opalescens* and *L. pealei* (see Drew, 1911; McGowan, 1954; Fields, 1965). This character needs to be reviewed further, and may prove to be variable across several (or most) loliginid species, potentially limiting its usefulness in cladistic analysis.
39. Spermatophore cement body ratio (oral portion longer than aboral portion/oral and aboral portions approximately equal in length/oral portion smaller than aboral portion) - Many of these data (and data for characters 40 and 41) have been coded directly into the matrix from Hess (1987).
40. Spiral filament in spermatophore (absent/present).
41. Oral component of spermatophore cement body (not divided/divided).

I. Miscellaneous

42. "Conus" (absent/present with edges fused/present, with edges unfused) - In species which possess internal, non-calcified shell remnants (pens or gladii), some possess a "secondary conus" (Toll, 1982) in which the posterior edges of the gladius are fused around the posterior visceral mass to form a cone. In some loliginids, the posterior edges of the gladius are curled ventrally and actually overlap ventrally, but are not fused. Most loliginids possess gladii which show only moderate ventral curling posteriorly (they lack a "conus").
43. Papillae on ink sac of males (absent/present) - Research on the genus *Loliolus* (Lu *et al.*, 1985) has shown that males of two species possess small pores on the ink sac. This characteristic has not been reported in any other loliginid species, and was not found in males of any other species examined in this study.
44. Cornea (absent/present) - The presence or absence of a corneal covering over the eye has been the nominal character separating the oegopsid squids from the myopsid squids.
45. Oviducts (both developed/only left oviduct developed).
46. Muscular septum in mantle cavity (absent/present) - Certain outgroup taxa (*Rossia, Euprymna*) possess a muscular septum dividing the mantle cavity longitudinally into two halves. Loliginids and other taxa in this study lack this feature.
47. Nuchal cartilage (absent/present).
48. Digestive gland (single/paired).

APPENDIX III. Material Examined. Material examined is listed by species name, ingroups first, in alphabetical order. The sex and approximate dorsal mantle length, when known, are listed for each specimen examined. (CAS, California Academy of Sciences; DML, dorsal mantle length; F, female; J, juvenile (sex not determined); M, male; NMNH, United States National Museum of Natural History; U, sex undetermined; UMML, University of Miami Invertebrate Museum).

Ingroup taxa

Alloteuthis africana Adam, 1950 - NMNH 727426 (1 M, 56 mm DML), NMNH BCF Table 6IX 6E-2-218 9-6-63 (2 M, 78 and 71 mm DML), UMML 1757 (1 F, 45 mm DML; 1 M, 58 mm DML).

A. media (Linné, 1758) - NMNH 817475 (3 F, 56, 64, and 67 mm DML; 2 M, 42 and 50 mm DML), UMML 1251.

A. subulata (Lamarck, 1798) - UMML 1252 (2 M, 100 and 101 mm DML), NMNH 817534 (1 F, 70 mm DML).

Loligo beka Sasaki, 1929 - UMML 1209 (1 F, 55 mm DML), UMML 1210 (1 M, 59 mm DML).

L. bleekeri Keferstein, 1866 - NMNH 332905 (1 J, 40 mm DML), UMML 1211 (2 M, 36 and 38 mm DML).

L. budo (Wakiya and Ishikawa, 1921) - UMML 1212 (1 F, 170 mm DML; 1 M, 190 mm DML).

L. chinensis Gray, 1849 - UMML PJ-102 (2 F, 75 and 107 mm DML), UMML PJ-110 (1 F, 92 mm DML).

L. duvauceli Orbigny, 1848 - NMNH 817827 (2 F, 100 and 123 mm DML), NMNH 817829 (1 M, 126 mm DML), NMNH 727560 (1 F, 110 mm DML), NMNH 727561 (2 M, 70 and 93 mm DML), NMNH 817823 (1 M, 66 mm DML), CAS 084583.

L. edulis Hoyle, 1885 - NMNH 814158 (4 M, 127, 133, 136, and 142 mm DML), CAS 030539 (2 M, 99 and 107 mm DML).

L. etheridgei (Berry, 1918) - UMML 1220 (1 F, 90 mm DML; 1 M, 104 mm DML).

L. forbesi Steenstrup, 1856 - NMNH (1 F, 133 mm DML).

L. gahi Orbigny, 1835 - UMML 2087 (1 F, 72 mm DML), UMML

2090 (2 F, 90 and 91 mm DML; 1 M, 69 mm DML).

L. japonica Hoyle, 1885 - NMNH 727551 (2 M, 75 and 77 mm DML), NMNH 332903 (3 M, 58, 70, and 77 mm DML), UMML 1224 (2 M, 61 and 68 mm DML), UMML 1226 (1 F, 60 mm DML).

L. kobiensis Hoyle, 1885 - UMML 31.2203 (1 F, 87 mm DML; 1 M, 76 mm DML).

L. ocula Cohen, 1976 - UMML 1683 (2 M, 53 and 62 mm DML), NMNH 727095 (2 M, 87 and 127 mm DML) (paratypes), NMNH 727096 (1 F, 89 mm DML).

L. patagonica (Smith, 1881) - UMML 1231 (1 F, 83 mm DML).

L. pealei LeSueur, 1821 - NMNH 730069 (2 M, 85 and 95 mm DML), NMNH 730531, NMNH 730183 (1 M, 206 mm DML), NMNH 814169 (1 F, 136 mm DML), NMNH 814191 (1 M, 90 mm DML; 1 J, 83 mm DML).

L. plei Blainville, 1823 - NMNH 574548 (1 M, 105 mm DML), NMNH 576456 (4 M, 146, 154, 195, and 217 mm DML), NMNH 813979 (2 M, 181 and 260 mm DML), NMNH 814288 (1 F, 120 mm DML; 1 M, 105 mm DML), NMNH 814316 (1 M, 198 mm DML), NMNH 814317 (1 M, 213 mm DML), NMNH 814318 (1 M, 197 mm DML), NMNH 814315 (1 M, 163 mm DML), NMNH 574320 (1 M, 169 mm DML), NMNH 574180 (2 M, 215 and 277 mm DML).

L. reesi (Voss, 1963) - UMML 1803 (1 M, 62 mm DML).

L. reynaudi Orbigny, 1845 - UMML 1233 (1 M, 175 mm DML), UMML 1234 (1 M, 95 mm DML).

L. roperi Cohen, 1976 - NMNH 575874 (1 M, 53 mm DML), UMML 933 (1 F, 38 mm DML; 2 M, 41 and 43 mm DML) (paratypes), UMML 1798 (1 M, 55 mm DML), UMML 72777 (1 M, 77 mm DML) (holotype).

L. sanpaulensis Brakoniecki, 1984 - UMML 1813 (2 M, 144 and 150 mm DML) (paratypes).

L. sibogae (Adam, 1954) - NMNH 575813 (1 F, 123 mm DML; 1 M, 139 mm DML).

L. singhalensis Ortmann, 1891 - UMML 31.2323 (1 M, 140 mm DML), UMML 2168 (1 M).

L. sumatrensis Orbigny, 1835 - NMNH 817821 (1 F, 52 mm DML), NMNH 817820 (1 F, 53 mm DML; 2 M, 48 and 50 mm DML).

L. surinamensis Voss, 1974 - UMML 2053 (1 F, 92 mm DML), UMML 31.2023 (2 F, 76 and 88 mm DML).

L. uyii Wakiya and Ishikawa, 1921 - CAS 035049, UMML 1239 (1 F, 94 mm DML; 1 M, 69 mm DML).

L. vossi (Nesis, 1982) - UMML 1259 (2 M, 65 and 78 mm DML).

L. vulgaris Lamarck, 1798 - UMML 1240 (1 M, 210 mm DML), UMML 1241 (1 F, 43 mm DML), UMML 1597 (1, 137 mm DML).

Loliolopsis diomedeae (Hoyle, 1904) - CAS 030492 (2 M, 38 and 41 mm DML), NMNH 576907 (2 F, 90 and 93 mm DML), NMNH 730085, UMML 31.697 (1 F, 102 mm DML), UMML (2 F, 95 and 104 mm DML), UMML 1799 (1 M, 83 mm DML).

Loliolus affinis (Steenstrup, 1856) - CAS 030250 (2 M, 21 and 25 mm DML).

L. hardwickei (Gray, 1849) - CAS 030251 (1 M, 40 mm DML), NMNH 817822.

L. noctiluca Lu, Roper, and Tait, 1985 - NMNH 00813974 (1 F, 68 mm DML; 3 M, 50, 51, and 56 mm DML).

Lolliguncula argus (Brakoniecki and Roper, 1985) - CAS 030252 (2 F, 43 and 43 mm DML; 1 M, 39 mm DML).

L. brevis (Blainville, 1823) - CAS 030491 (2F, 42 and 43 mm DML), NMNH 884122 (1 M, 66 mm DML).

L. mercatoris Adam, 1941- UMML 1244 (1 M), UMML 31.790 (1 M, 15 mm DML), UMML 31.2550 (1 M, 21 mm DML).

L. panamensis Berry, 1911 - CAS 030157 (1 M, 44 mm DML), CAS 030495 (2 F, 86 and 105 mm DML).

Pickfordiateuthis pulchella (Voss, 1953) - UMML 1948 (20 mm DML).

Sepioteuthis australis Quoy and Gaimard, 1832 - NMNH 816311 (1 F, 102 mm DML).

S. lessoniana Lesson, 1830 - CAS 030624 (2 F, 93 and 105 mm DML), NMNH 297637 (2 M, 127 and 166 mm DML), NMNH CH6-7 (1 M, 155 mm DML).

S. loliginiformes (Rüppell and Leuckart, 1828) - NMNH 730575 (1, 17 mm DML).

S. sepioidea (Blainville, 1823) - CAS 030428 (1 M, 72 mm DML), NMNH 576881 (1 M, 101 mm DML), NMNH 9548 (2 M, 99 and 106 mm DML), NMNH 576877 (1 M, 110 mm DML), NMNH 814382 (1 F, 119 mm DML).

Uroteuthis bartschi Rehder, 1945 - CAS 030485 (1 M, 104 mm DML), NMNH 575388 (1 M, 122 mm DML), UMML 1255 (2 F, 119 and 121 mm DML).

Outgroup taxa

Bathyteuthis berryi Roper, 1968 - NMNH 727573 (1 M, 47 mm DML).

Ctenopteryx sicula (Vérany, 1851) - NMNH 728929, NMNH 727721, NMNH 730695 (1 U, 68 mm DML), NMNH 728935 (2 U, 21 and 45 mm DML), NMNH 730696 (1 U, 75 mm DML), NMNH 730697 (1 M, 81 mm DML), NMNH 730698 (1 F, 52 mm DML).

Euprymna moresi (Verrill, 1881) - CAS 021433 (1 F, 31 mm DML; 1M, 33 mm DML).

E. scolopes (Berry, 1913) - CAS 030512 (2 U, 24 and 28 mm DML), CAS 030751 (1 U, 30 mm DML).

Rossia pacifica Berry, 1911 - CAS 030356 (2 F, 30 and 30 mm DML), CAS 081003 (1 U, 50 mm DML).

Sepia aculeata Orbigny, 1848 - CAS 084742 (1 M, 210 mm DML).

Moroteuthis robusta (Dall in Verrill, 1876) - CAS 030111 (partial specimen, total length 9 ft., 7 inches), CAS 035031 (1 U, 300+ mm DML).

Todarodes pacificus (Steenstrup, 1880) - CAS 024414 (2 U, 151 and 155 mm DML), CAS 024415 (1 U, 166 mm DML), CAS 030961, CAS 031020 (1 U, 106 mm DML).